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Research Article

Habitat selection of the mud crab *Rhithropanopeus harrisii* in its newly invaded range

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Abstract

Information on the habitat selection by non-indigenous species is crucial for understanding their effects on the communities to which they are introduced, since the effects are often focused on the invaded habitats. The North American mud crab *Rhithropanopeus harrisii* is a new invader in the northern Baltic Sea, on the coasts of Finland and Estonia. In the Finnish Archipelago Sea, it has been found in two very distinct habitats: reed belts of *Phragmites australis* and algal zones with *Fucus vesiculosus* as the main habitat-forming species. In previous studies in the Baltic Sea, *R. harrisii* has preferred *F. vesiculosus* and has locally driven a shift in the structure of *F. vesiculosus*-associated invertebrate communities. Here, we disentangled whether habitat choice was determined by habitat structure or the availability of food. First, we conducted a habitat selection experiment with *P. australis* and *F. vesiculosus* habitats and varying food availability, and found that *R. harrisii* preferred *F. vesiculosus*, with food having no effect on the habitat choice. Second, we studied if the preference for *F. vesiculosus* was due to the alga itself or the rocks it grows on. We found that *R. harrisii* preferred the shelter of the rock habitat, indicating that *R. harrisii* choose their habitat based on habitat structure rather than food availability in the habitat. However, the preference for sheltered rocky bottom habitats also exposes the associated *F. vesiculosus* communities to the impacts of *R. harrisii* through predation.

Key words: non-indigenous species, habitat selection, laboratory, Baltic Sea, Decapoda, *Fucus vesiculosus*

Introduction

Non-indigenous species can alter biotic and abiotic conditions, species composition, and food chain function in their new environments (Ruiz et al. 1997; Leppäkoski et al. 2002; Bax et al. 2003; Molnar et al. 2008). Although the impacts of invasion can be seen throughout the ecosystem, the effects are often focused on the invaded habitats. Information on the habitat selection by non-indigenous species is, therefore, crucial for understanding their effects on the communities to which they are introduced. Habitat selection experiments in controlled settings enable detection of direct effects and allow for the prediction of indirect and more far-reaching impacts of non-indigenous species on the ecosystems.

In marine environments, marine traffic is globally the most significant vector in spreading non-indigenous species (Ruiz et al. 1997; Leppäkoski et al. 2002; Bax et al. 2003; Molnar et al. 2008). The Baltic Sea is one of the busiest shipping routes in the world (Eriksson et al. 2004) and the world's largest brackish water sea. As the majority of the world's harbors are located at estuaries, most species introduced to the Baltic Sea also originate from brackish waters (Leppäkoski et al. 2002) and are, therefore, already adapted to similar conditions. As a whole, species in the Baltic Sea are mostly remnants from different phases of its history and spread out from the North Atlantic, or were introduced as non-indigenous species (Leppäkoski et al. 2002). Due to gradients in salinity and temperature, and the unevenness of the seafloor, the Baltic Sea houses a wide range of biotopes, making it more probable for non-indigenous species to arrive at a suitable habitat in the new environment (Leppäkoski et al. 2002). As of 2015, there were 133 non-indigenous species in the Baltic Sea (AquaNIS 2015).

One recent invader in the Baltic Sea is the North American mud crab *Rhithropanopeus harrisii* (Gould, 1841). It is a small, omnivorous benthic crustacean, originating from the Atlantic coasts of North America with a native distribution range from Canada to Mexico (Rodríguez and Suárez 2001). Nowadays, it occurs throughout the coasts of the Northern Hemisphere (Boyle et al. 2010). *R. harrisii* was first found in the Baltic Sea in 1936 (Schubert 1936), and the first observation in Finland, northern Baltic Sea, was made in the Archipelago Sea in 2009 (Karhilahti 2010). Today, *R. harrisii* has formed quite dense reproducing populations in the Archipelago Sea, and its distribution is increasing along the coast further to the north (Fowler et al. 2013; Forsström et al. 2015; see Gagnon and Boström 2016 for map of recent distribution).

In its native range, *R. harrisii* is found in a wide variety of shelter-offering habitats, for example in oyster reefs, eelgrass beds, and debris (Ryan 1956; Petersen 2006; Fowler et al. 2013; J.M. Hanson, Gulf Fisheries Centre, Moncton, Canada, personal communication). In non-native ranges, *R. harrisii* can similarly be found in habitats that offer shelter, such as on sand and silt bottoms with shells, among living and decaying vegetation, and under stones and woody debris (Boyle et al. 2010; Turoboyski 1973; Roche and Torchin 2007). In the Finnish Archipelago Sea, *R. harrisii* has been found in a variety of habitats: on mud and sand bottoms, under small stones, inside dead *Phragmites australis* ((Cav.) Trin. ex Steud.) reeds, amongst *Fucus vesiculosus* (Linnaeus, 1753), and even on rocky shores exposed to waves, indicating the use of any structured habitat they can find (Fowler et al. 2013).

Fucus vesiculosus, one of the habitats *R. harrisii* commonly inhabits in the Baltic Sea, is a brown alga and a keystone species in the Baltic Sea. It grows on rocky bottoms and houses a diverse community of macrofauna and epiphytic flora (Kautsky et al. 1992). Recently, a drastic effect of *R. harrisii* on the *F. vesiculosus* communities was reported by Jormalainen et al. (2016). Interestingly, the tendency to inhabit stands of *F. vesiculosus* has not, to our knowledge, been observed in other parts of *R. harrisii* occurrence range. In the northern Baltic Sea, *R. harrisii* also occurs in high frequencies on shallow, soft sediment shores, with dense belts of reed *Phragmites australis*. These reed belts are very common and overgrow other vegetation types of the shoreline, and there are harvest attempts to constrain their coverage (Ikonen and Hagelberg 2007). However, reed belts also provide important habitats for a variety of fauna (Long et al. 2011; R. Puntila, Marine Research Center, Finnish Environment Institute, Helsinki, Finland, unpublished data) as well as spawning areas for several species of fish (Kallasvuo et al. 2011).

Here, we studied the habitat selection of *R. harrisii* by focusing on two important environments in the northern Baltic Sea: *F. vesiculosus* and *P. australis*. Habitat selection may be based on food or shelter (Lima and Dill 1990), and disentangling these factors is difficult, especially with species using a host plant as shelter but also feeding on it or on the associated fauna. First, we examined *R. harrisii* habitat preference between *P. australis* reeds and *F. vesiculosus* algal stands, and aimed to determine whether their habitat choice was based on food by simultaneously controlling food availability in the habitats. Second, *F. vesiculosus* habitats in nature also provide shelter, both within the dense algal bushes and under the rocks it grows attached to. Therefore, we further evaluated habitat choice between the structural shelter of bare rocks and stems of *F. vesiculosus*. Finally, as size (for example Richards 1992; Fernandez et al. 1993) and sex (Vesakoski et al. 2008; Bartolino et al. 2011) of an animal may affect its habitat choice, we also controlled for these factors.

Material and methods

We conducted two experiments to study whether *R. harrisii* habitat selection is based on food availability or habitat structure. In the food availability experiment, we used *F. vesiculosus* and *P. australis* vegetation habitats common in the Archipelago Sea. In the habitat structure experiment, the habitats were *F. vesiculosus* habitat and a rock habitat. We used different habitats between the two experiments to first mimic the abundance of food in the two vegetation habitats, and second, based on the results of the food availability experiment, to distinguish between the different structures of the *F. vesiculosus* habitats in nature, namely the *F. vesiculosus* algal stands and rocks to which they grow attached. Habitat selection was studied by building the habitats in aquaria. In both experiments, the two different habitats were present in each tank.

The experiments were conducted in August 2013 at the Archipelago Research Institute (University of

Turku) in stable laboratory conditions. Both temperature and the light-dark cycle in the laboratory followed the ambient conditions: temperature was kept at 17–19 °C (seawater temperature at shoreline) and light-dark cycle at 16:8 hours (light from 0600 h until 2200 h).

We collected *R. harrisii* crabs from the Archipelago Sea between June and August 2013. Prior to the experiments, we determined the sex of the crabs and measured their carapace width (CW; in mm). Only non-ovigerous females were used in the experiment. The crabs were kept in flow-through tanks and fed chironomid larvae *ad libitum*. Before entering the experiment, each crab was deprived of food for 24 hours.

Habitat choice based on food availability

First, we studied *R. harrisii* habitat preference between *F. vesiculosus* and *P. australis* habitats and the effect of food availability on habitat preference. The habitats were built in aquaria and consisted of 5 branches of *F. vesiculosus* and 10 stems of *P. australis* reeds, both in an oval-shaped clump a minimum of 5 cm away from the walls and corners of the tanks. The habitats were placed at the opposite ends of the tank, and separated by an open area of sand. We washed the *F. vesiculosus* branches with warm freshwater to remove any animals, and attached them to small rocks with a rubber band. *P. australis* reeds were also washed and cut to an approximate size of 20 cm. The bottom of each tank was covered with 2 cm of washed sand to allow the burrowing behavior of the crabs, and to bury the rocks with attached branches of *F. vesiculosus* so that only the *F. vesiculosus* branches were left visible above sand, and to keep the *P. australis* reeds upright by inserting them into the sand. We used in total 74 *R. harrisii* individuals, each individual alone in a tank sized 98 × 27 × 45 cm (120 liters). We controlled for the size and sex of the crab by using small (6.1–10.0 mm CW), medium-sized (10.1–14.0 mm CW) and large (14.1–18.0 mm CW) individuals and an equal number of males and females in this experiment. Each size class and both sexes received equal replication in each food availability treatment.

To determine the effect of food availability on *R. harrisii* habitat choice, we used 4 food availability treatments: 1) food in the *F. vesiculosus* habitat, 2) food in the *P. australis* habitat, 3) food in both habitats (positive control), and 4) no food in either of the habitats (negative control). As the food item, we used the blue mussel *Mytilus trossulus* (Gould, 1850), a part of *R. harrisii* diet in the Baltic Sea (see for example Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009; Forsström et al. 2015). The mussels, sized 2–2.5 cm, were placed in hair rollers sealed with mesh, allowing the scent to get through but preventing the crabs from eating the mussels. Empty but otherwise similar hair rollers were placed in the habitats with no food, so that in both habitats in each tank there was one hair roller either containing the food item or not. Mussel size was within the size range that our large crabs could likely have consumed (Milke and Kennedy 2001, referenced in Forsström et al. 2015), could they have reached the mussel through the hair roller. The mussels were, however, only used to provide the scent of food. Food items or empty hair rollers were placed in the habitats five minutes prior to releasing the crab in the tank, allowing the scent to reach the bottom of the tank.

The experiment was run in six trials consisting of 12 tanks (= 12 individuals). We ran three replications of each treatment simultaneously, thus, each treatment was replicated 18 times. As two individuals were lost, we ran an additional seventh trial with only 2 tanks to replace lost individuals. Finally, 1 observation was removed from the analyses (see Statistical analyses below), resulting in a total of 71 individuals.

To avoid systematic error in crab behavior in response to the observers, the walls of the tanks were covered with sheets cut from black plastic bags and the placement of the habitats was randomized. The tanks were filled with ambient seawater (salinity 5.5), which was changed between trials and aerated before the start of each trial. Between the trials, the vegetation and stones were removed and the habitats rebuilt to avoid pseudoreplication.

In the beginning of each trial, at 2000 h, one crab per tank was released to the bottom and center of the tank. The crabs were left undisturbed until 0800 h at which time we recorded their location as the habitat choice. Possible locations were: in the *F. vesiculosus* or *P. australis* habitat (attached or right next to vegetation), on sand, or next to a wall (crab in corner or next to tank wall). The morning observation was used to represent habitat choice, as in a pilot experiment, we found that after releasing the crabs, they were either immobile for a long period of time or did not settle at all while observed. We also noted a clear diurnal rhythm, with the crabs being active during the night. Thus, to measure selective and not random habitat choice, the crabs were left to explore the tanks overnight.

Habitat choice based on habitat structure

To further disentangle whether habitat choice was guided by habitat structure, we used a *F. vesiculosus* habitat and a rock habitat, as rocks are a structurally different habitat type and the cavities underneath may provide better shelter for the crabs. A branch of *F. vesiculosus* was placed at one end of the tank and three rocks at the other, both away from the walls of the tank. For the rock habitat, we collected rocks of 3–5 cm in diameter and washed them with warm freshwater. Here, we used 40 *R. harrisii* individuals (20 males, 20 females) with sizes ranging from 7.6 mm to 12.9 mm CW. Again, each crab was placed individually in a tank sized 39 × 21 × 25 cm (20 liters). The experiment was run in 4 trials, with 10 tanks (= 10 individuals) per trial.

As in the food availability experiment, the experiment started at 2000 h by placing the crabs to the middle of the tanks, and their locations were recorded at 0800 h. The possible locations were: in the *F. vesiculosus* habitat (attached or right next to vegetation), in the rock habitat (right next to or under the rocks), on sand, or next to a wall (crab in corner or next to tank wall).

Statistical analyses

Besides occurring in the habitats, many of the crabs were found in the corners or next to tank walls. Naturally, the walls of the tank are not habitat in similar manner as *F. vesiculosus*, *P. australis*, or rock habitat, but for simplicity, we used next to wall as an alternative "habitat" in the analyses. We merged all observations of the crabs next to the walls of the tank into one next to wall "habitat" for both experiments, as the crabs occurred in corners and next to tank walls equally in all habitats of both experiments (data not shown). As only one crab was found on sand, this observation was removed from the data, resulting in 71 crabs in the food availability experiment and 40 crabs in the habitat structure experiment.

We analyzed both the food availability experiment data and the habitat structure experiment data in a similar manner. First, we studied the overall preference for each habitat with frequency analyses. These alternative habitats were *F. vesiculosus* habitat, *P. australis* habitat, and next to tank wall in the food availability experiment, and *F. vesiculosus* habitat, rock habitat, and next to tank wall in the habitat structure experiment. Second, we modelled the occurrence in each habitat in relation to the explanatory factors using generalized linear models.

Firstly, we analyzed simply the frequencies of occurrence of the crabs in different habitats using a chi-square test. As the overall chi-square test does not show statistical significance between habitat pairs, we further conducted chi-square tests for each pair of habitats.

Secondly, we determined which factors influenced the habitat choice using generalized linear models with binomial distributions (procedure GLIMMIX in SAS 9.4 [SAS Institute Inc. 2002–2014]). To get binary response variables instead of multinomial responses, we created three new response variables in the food availability experiment: crab occurrence in *F. vesiculosus* versus in other habitats, crab occurrence in *P. australis* versus in other habitats, and crab occurrence next to tank wall versus in other habitats. Similarly, three new response variables (crab occurrence in rock habitat versus in other habitats, crab occurrence in *F. vesiculosus* versus in other habitats, and crab occurrence next to tank wall versus in other habitats) were created for the habitat structure experiment. Merging the two habitats allowed us to study the occurrence in one habitat compared to all other habitats and to avoid problems caused by multinomial response variables. We used the location of the crab in the morning as a binary response variable and sex and size as explanatory variables in the analyses of both experiments, and food availability as an explanatory variable in the analyses of the food availability experiment. The models produced probabilities of crab occurrence in each habitat compared to all other habitats. Model selection was done by comparing the AICc values. Interactions between explanatory variables decreased model fit and were left out of the final models. Trial was used as a random factor in all analyses, but it decreased model fit and was, therefore, left out of the final models. In the food availability experiment, pairwise comparisons between the food availability treatments were controlled for False Discovery Rate (FDR) to decrease the probability of type I error. A P-value of 0.05 was used to determine if the differences were statistically significant.

Results

Habitat choice based on food availability

In the food availability experiment, frequencies of crab occurrence between the habitats differed significantly from each other (Figure 1; N = 71, DF = 3, $\chi^2 = 48.15$, $P < 0.0001$). Frequencies of occurrence also differed significantly between all habitat pairs. 61% of *R. harrisii* individuals were found in the *F. vesiculosus* habitat, whereas only 11% of the crabs were found in the *P. australis* habitat, making it the least favored habitat.

When examining the effect of explanatory variables on habitat choice, food availability or sex of the crab had no effect on the habitat choice of *R. harrisii* (Table 1). Crab occurrence in any of the habitats was

Table 1. The effects of different explanatory variables on the habitat choice of *R. harrisii* in the generalized linear models. Crab location in the morning as a binary variable is used as the response variable for habitat choice. Bold and italicized P-value denotes statistical significance; italicized P-value indicates a trend.

Habitat choice based on food availability			
Explanatory variable	*DF*	*F*	*P*
F. vesiculosus against *P. australis* and next to wall "habitat"			
Food	3, 65	1.92	0.135
Sex	1, 65	2.30	0.134
Size	1, 65	1.62	0.208
P. australis against *F. vesiculosus* and next to wall "habitat"			
Food	3, 65	0.16	0.924
Sex	1, 65	2.13	0.149
Size	1, 65	1.92	0.171
Next to wall "habitat" against *F. vesiculosus* and *P. australis*			
Food	3, 65	1.18	0.325
Sex	1, 65	0.42	0.518
Size	1, 65	5.29	***0.025***
Habitat choice based on habitat structure			
Explanatory variable	*DF*	*F*	*P*
Rock against *F. vesiculosus* and next to wall "habitat"			
Sex	1, 37	0.41	0.527
Size	1, 37	1.86	0.181
F. vesiculosus against rock and next to wall "habitat"			
Sex	1, 37	0.32	0.575
Size	1, 37	0.64	0.429
Next to wall "habitat" against *F. vesiculosus* and rock			
Sex	1, 37	1.12	0.294
Size	1, 37	3.61	*0.065*

not influenced by the availability or lack of food in the habitat (Figure 2). When comparing the next to wall occurrence as a habitat with the occurrence in the two vegetation habitats combined (next to wall against *F. vesiculosus* and *P. australis*), the size of the crab had a significant effect on habitat choice (Table 1): the probability to end up next to a wall increased with increasing size of the crab (Figure 3). Size of the crab did not affect the preference for *F. vesiculosus* or *P. australis* habitat.

Habitat choice based on habitat structure

In the habitat structure experiment, frequencies of crab occurrence between the habitats differed significantly from each other (Figure 4; N = 40, DF = 2, χ^2 = 11.1, P = 0.0038) and between all habitat pairs. The rock habitat was preferred over others, with 65% of *R. harrisii* occurring there. The *F. vesiculosus* habitat was the least favored of all habitats, with only 8% of the crabs settling in the *F. vesiculosus* habitat.

When studying the impact of sex and size of the crab on habitat choice, we found a slight effect of size: regarding next to a wall as a habitat, larger crabs were found next to a wall more often than smaller crabs in the generalized linear model (Table 1;

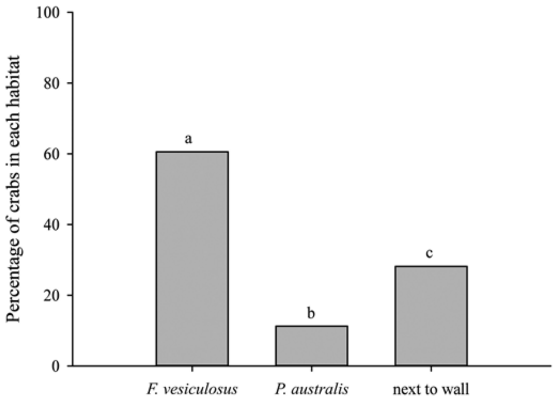

Figure 1. *R. harrisii* occurrence in each habitat by percentage in the food availability experiment with *F. vesiculosus* and *P. australis* habitats (N = 71). Next to wall observations are considered an alternative "habitat". Lower case letters denote statistically significant difference between each habitat in the chi-square tests for the habitat pairs.

Figure 5), but this trend was only nearly significant. Otherwise, size and sex of the crab had no effect on their habitat choice (Table 1).

Discussion

In this habitat selection study, we found no effect of food availability on *R. harrisii* habitat choice, but instead, habitat choice was guided by habitat structure. Two other recent *R. harrisii* studies (Nurkse et al. 2015; Aarnio et al. 2015) also found an indication for a preference of shelter over food. First, Nurkse et al. (2015) studied habitat choice using various habitat alternatives, and found that *R. harrisii* preferred rocks with attached *F. vesiculosus* over bare rocks and other habitats. They suggested that this combination of *F. vesiculosus* and rock would provide more shelter than the other habitat alternatives. Furthermore, supporting our results, Nurkse et al. (2015) did not find food availability to affect *R. harrisii* preference for *F. vesiculosus*. Second, in a study by Aarnio et al. (2015), *R. harrisii* preferred *F. vesiculosus* over mud. When given a choice between prey species characteristic to the two studied habitats, *R. harrisii* showed no preference, indicating that the preference for *F. vesiculosus* was as well caused by the shelter it provides (Aarnio et al. 2015).

The preference for shelter over food can be seen as a result of the trade-off between maximizing food intake and minimizing predation risk (Sih 1980; Dill 1987; Lima and Dill 1990; Verdolin 2006). There is a lack of studies assessing the relative importance of food and shelter to aquatic animals, but there are studies focusing on fitness effects related to choosing the sheltered habitat. Other benthic crustaceans have been found to favor more sheltered habitats to avoid predation: very small juveniles of the American lobster *Homarus americanus* (H. Milne Edwards, 1837) and the Jonah crab *Cancer borealis* (Stimpson, 1859) preferred shelter-providing habitats over open habitats (Wahle and Steneck 1992; Richards 1992), and very small lobsters, when exposed, were indeed found to be more vulnerable to predator attacks (Wahle and Steneck 1992). Dungeness crabs *Metacarcinus magister* (Dana, 1852) preferred a habitat consisting of oyster shells over eelgrass *Zostera marina* (Linnaeus, 1753) and eelgrass over mud, with the highest mortality in the mud habitat and lowest in oyster shells (Fernandez et al. 1993). In aquatic environments, preference for sheltered habitats with lower predation risk is not limited to benthic crustaceans. Pinfish *Lagodon rhomboides* (Linnaeus, 1766) preferred sheltered seagrass habitats to open sandflats (Levin et al. 1997), but in aquaria experiments, in the absence of predation, showed no preference for either habitat (Jordan et al. 1997). However, when a predator was introduced, pinfish settled to a vegetated habitat (Jordan et al. 1997). Similarly, pre-adaptation to predator avoidance in the northern Baltic Sea could also be the cause of the shelter-seeking behavior of *R. harrisii*.

Primary preference for shelter is also logical for a mobile animal able to look for food elsewhere, such as in the *F. vesiculosus* algal stands on rocky bottoms, while hiding in the cavities under rocks. However, the cavities under rocks are not necessarily nutritionally poor places as other animals also use them as shelter. Preference for rocky bottom habitat and cavities under the rocks may have ecological consequences by producing new competitive and predatory interactions between the non-indigenous crab and cavity-breeding fish. For example, an amensalistic interaction between *R. harrisii* and cavity-breeding sand gobies *Pomatoschistus minutus* (Pallas, 1770) has already been found in the northern Baltic Sea (T. Lehtonen, O. Vesakoski, J. Yli-Rosti, A. Saarinen, K. Lindström, University of Turku, Turku, Finland, Monash University, Melbourne, Australia, and Åbo Akademi University, Turku, Finland, unpublished data).

Other factors like size and sex may also affect habitat choice. In our study, larger *R. harrisii* individuals were found next to the walls of the tanks more often than smaller ones, although size did not affect the preference for the studied habitats. Size-related behavioral differences have also been found with the Jonah crab and juvenile Dungeness crabs. Small Jonah crabs preferred to hide in cobble while

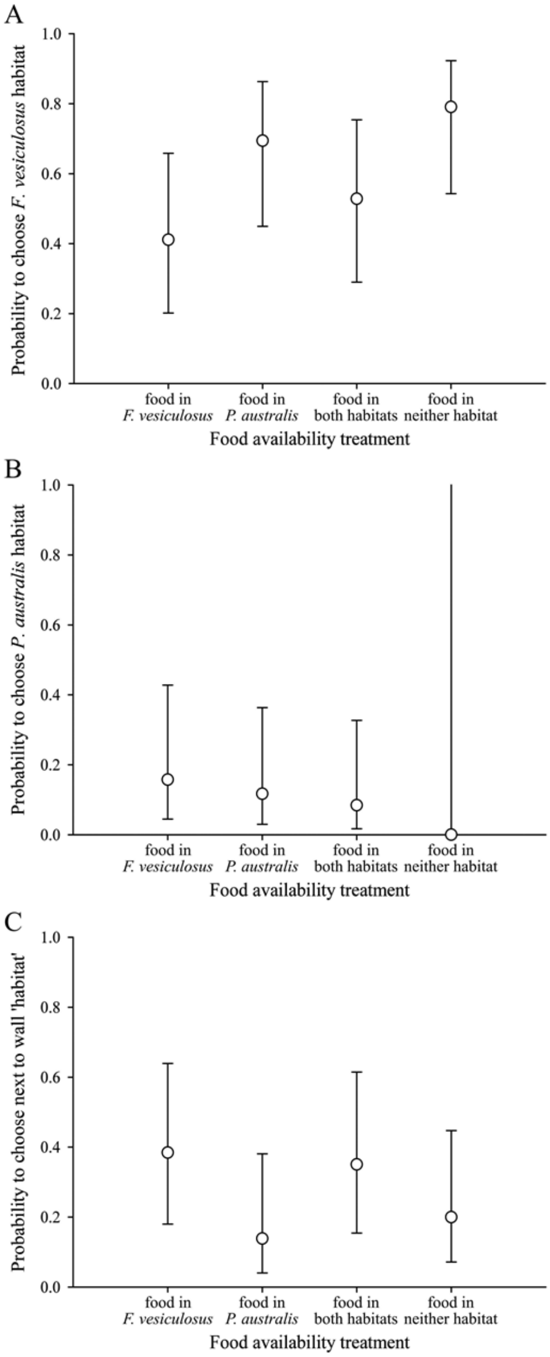

Figure 2. The effect of food availability on *R. harrisii* habitat choice. The probability of crab occurrence in A) *F. vesiculosus* habitat, B) *P. australis* habitat, and C) next to wall "habitat" was analyzed using generalized linear models with crab location as the response variable and food availability as one of the explanatory variables. Food availability was manipulated with four food availability treatments: food in *F. vesiculosus* habitat, food in *P. australis* habitat, food in both habitats, and no food in either habitat. After FDR correction, food availability did not affect habitat choice. N = 71. Error bars represent 95 % confidence limits (CL).

bigger ones were found equally on sand and in cobble (Richards 1992). Smaller Dungeness crab juveniles also preferred more sheltered eelgrass habitat over mud (Fernandez et al. 1993). We hypothesize that the larger crabs' tendency to settle next to a wall in this study more likely reflects behavioral differences between the sizes than actual habitat choice, although the size of the crab was clearly significant only in the experiment with varying food availability. The reduced significance in the experiment with different habitat structures is, however, likely due to the smaller size of the individuals used in the latter experiment. The repetitive results of these experiments could indicate a behavioral pattern. It is also possible that, in our study, the smaller *R. harrisii* individuals could hide more efficiently between rocks and among branches of *F. vesiculosus* than the bigger crabs, thus getting shelter from the habitat provided by the set-up. Smaller amphipods, for example, have also been found to prefer densely branched algal mimics as habitat over more sparsely branched mimics (Hacker and Steneck 1990). It could also be that the larger crabs were more likely to end up next to tank walls when searching for alternative environments, while the smaller crabs tend to stay in the shelter they have found.

We did not detect any effect of the sex of the crab on their habitat choice, but such differences may exist in nature, and have been found for example in the isopod *Idotea balthica* (Pallas, 1772) (Vesakoski et al. 2008). Differences in habitat preference between males and females are usually due to different trade-offs between nutrition and predation risk to maximize reproductive success (Vesakoski et al. 2008; Bartolino et al. 2011). The lack of differences between the sexes in *R. harrisii* behavior in this study therefore suggests equal trade-offs between food and shelter for both sexes. We used only non-ovigerous females in the experiments, and it is possible that the habitat choice of ovigerous females could differ from that of males and non-ovigerous females. Indeed, we expect that the trade-off between food and shelter would be even more strongly towards shelter in ovigerous females. For example, ovigerous females of the intertidal crab *Neohelice granulata* (Dana, 1851) are more abundant in sheltered salt marshes than on mudflats and are far less active than both males and non-ovigerous females (Luppi et al. 2013). Similarly, ovigerous females of the fiddler crab *Minuca burgersi* (Holthuis, 1967) do not leave their burrow, to minimize predation risk (Benetti et al. 2007), and ovigerous Dungeness crabs tend to aggregate in burrows on silty sand habitats, whereas males and non-ovigerous females use a wider variety of habitats (Stone and O'Clair 2001).

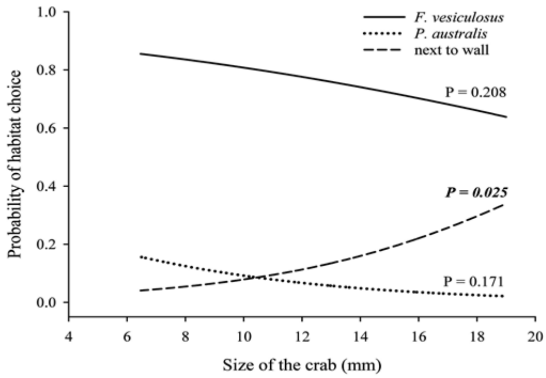

Figure 3. The effect of size of *R. harrisii* individuals on their habitat choice in the generalized linear models of the food availability experiment with *F. vesiculosus* and *P. australis* habitats (N = 71). Crab location is used as the response variable and size of the crab as an explanatory variable. Bold and italicized P-value denotes statistical significance.

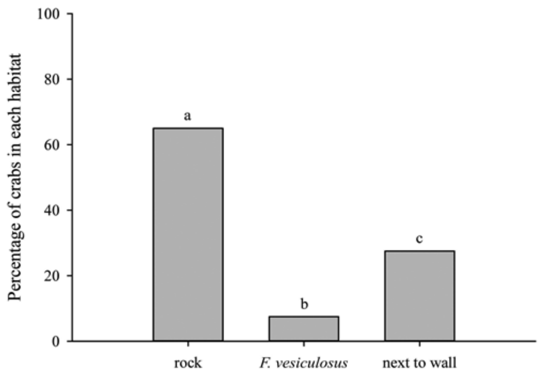

Figure 4. *R. harrisii* occurrence in each habitat by percentage in the habitat structure experiment with *F. vesiculosus* and rock habitats (N = 40). Next to wall observations are considered an alternative "habitat". Lower case letters denote statistically significant difference between each habitat in the chi-square tests for the habitat pairs.

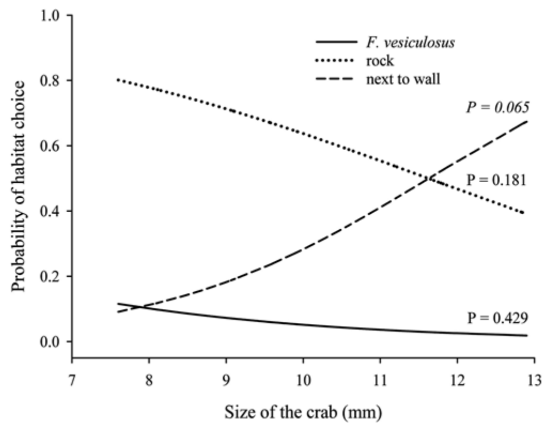

Figure 5. The effect of size of *R. harrisii* individuals on their habitat choice in the generalized linear models of the habitat structure experiment with *F. vesiculosus* and rock habitats (N = 40). Crab location is used as the response variable and size of the crab as an explanatory variable. Italicized P-value indicates a trend.

Interestingly, we found that *R. harrisii* preferred *F. vesiculosus* habitat over *P. australis* reed habitat, even though in nature the crabs can be very abundant on mud bottoms harboring dense reed belts of *P. australis*. Observed densities have reached up to an average of 75 individuals/m^2 in reeds, whereas no crabs were found on open mud bottoms (Sjöroos 2016). It could be that the vertical reed stands of our set-up did not provide enough shelter for the crabs, but instead, the dense layer of decaying reeds by the bottom is the attractive habitat for the crabs in nature. In the southern Baltic Sea, *R. harrisii* have also been found on bottoms covered with vascular plants (Janas and Kendzierska 2014). However, they also occupy bottoms free of vegetation (Janas and Kendzierska 2014), with higher densities on muddy bottoms, although the occurrence is patchy (Hegele-Drywa and Normant 2014). In addition, we have noted that, if disturbed, *R. harrisii* tend to bury themselves in sand or silty sand, meaning that the sand and mud bottoms common in the Archipelago Sea also provide hiding places for the crabs. However, in our experiment, *R. harrisii* did not choose the open sand habitat, as only one individual was found on sand. Open soft sediment habitats have not been favored by *R. harrisii* in previous experimental studies by Aarnio et al. (2015) or Nurkse et al. (2015) either. This discrepancy between observations in nature and laboratory experiments requires further study.

In conclusion, our results combined with earlier ones suggest that, in nature, *R. harrisii* does not appear to choose habitat based on food availability, but instead, the shelter-offering structure of habitat has a greater impact on its habitat choice. In the northern Baltic Sea, algal stands of *F. vesiculosus* provide additional shelter in the rocky bottom habitats, and occurring in these habitats, *R. harrisii* likely prefers hiding under the rocks rather than within the *F. vesiculosus* bushes. While hiding under rocks, the crabs nevertheless prey on the invertebrate species of *F. vesiculosus* communities as shown by isotope analyses (Aarnio et al. 2015) and laboratory experiments (Forsström et al. 2015) as well as field studies (Forsström et al. 2015; Jormalainen et al. 2016). Forsström et al. (2015) and Jormalainen et al. (2016) found the increase in the number of *R. harrisii* to decrease the abundance of *Theodoxus fluviatilis* (Linnaeus, 1758), a small gastropod grazing on the epiphytic algae growing on *F. vesiculosus*. As increased epiphytic growth reduces the growth and reproductive success of *F. vesiculosus* (Honkanen and Jormalainen 2005; Korpinen et al. 2007), such effect may be detrimental to *F. vesiculosus*. However, *R. harrisii* also feeds on crustacean grazers, for example, the isopod *Idotea balthica*, which can consume almost entire belts of *F. vesiculosus* when occurring in large numbers in autumn (Haavisto and Jormalainen 2014). Overall, however, Jormalainen et al. (2016) showed that an increase in the number of *R. harrisii* over a 3-year period coincided with a fall in biodiversity and a shift in the community structure of the *F. vesiculosus*-associated invertebrate community. In all, the effects of *R. harrisii* on these communities are of interest because of the ecological importance of *F. vesiculosus* as the main habitat-forming species on the rocky bottoms of the northern Baltic Sea. However, for creating a full picture on their ecosystem-wide effects, detailed information is needed also on their behavior in other habitat types, such as soft bottoms with less natural cavities to use as hiding places, where the effects may greatly differ from the effects on rocky bottom communities.

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References

Aarnio K, Törnroos A, Björklund C, Bonsdorff E (2015) Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea. *Aquatic Invasions* 10: 399–413, https://doi.org/10.3391/ai.2015.10.4.04

AquaNIS (2015) Information system on Aquatic Non-Indigenous and Cryptogenic Species. World Wide Web electronic publication. http://www.corpi.ku.lt/databases/aquanis Version 2.36+ (accessed 19 December 2016)

Bax N, Williamson A, Aguero M, Gonzalez E, Geeves W (2003) Marine invasive alien species: a threat to global biodiversity. *Marine Policy* 27: 313–323, https://doi.org/10.1016/S0308-597X(03)00041-1

Bartolino V, Ciannelli L, Bacheler NM, Chan K (2011) Ontogenetic and sex-specific differences in density-dependent habitat selection of a marine fish population. *Ecology* 92: 198–200, https://doi.org/10.1890/09-1129.1

Benetti AS, Negreiros-Fransozo ML, Costa TM (2007) Population and reproductive biology of the crab *Uca burgersi* (Crustacea: Ocypodidae) in three subtropical mangrove forests. *Revista de Biología Tropical* 55: 55–70, https://doi.org/10.15517/rbt.v55i0.5806

Boyle T, Keith D, Pfau R (2010) Occurrence, reproduction, and population genetics of the estuarine mud crab, *Rhithropanopeus harrisii* (Gould) (Decapoda, Panopidae) in Texas freshwater reservoirs. *Crustaceana* 83: 493–505, https://doi.org/10.1163/001121610X492148

Czerniejewski P, Rybczyk A (2008) Body weight, morphometry, and diet of the mud crab *Rhithropanopeus harrisii tridentatus* (Maitland, 1874) in the Odra estuary, Poland. *Crustaceana* 81: 289–1299, https://doi.org/10.1163/156854008X369483

Dill LM (1987) Animal decision-making and its ecological consequences: the future of aquatic ecology and behavior. *Canadian Journal of Zoology* 65: 803–811, https://doi.org/10.1139/z87-128

Eriksson BK, Sandström A, Isæus M, Schreiber H, Karås P (2004) Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. *Estuarine, Coastal and Shelf Science* 61: 339–349, https://doi.org/10.1016/j.ecss.2004.05.009

Fernandez M, Iribarne O, Armstrong D (1993) Habitat selection by young-of-the-year Dungeness crab *Cancer magister* and predation risk in intertidal habitats. *Marine Ecology Progress Series* 92: 171–177, https://doi.org/10.3354/meps092171

Forsström T, Fowler AE, Manninen I, Vesakoski O (2015) An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisii* in the Northern Baltic Sea. *Biological Invasions* 17: 2729–2741, https://doi.org/10.1007/s10530-015-0909-0

Fowler AE, Forsström T, von Numers M, Vesakoski O (2013) The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquatic Invasions* 8: 89–96, https://doi.org/10.3391/ai.2013.8.1.10

Gagnon K, Boström C (2016) Habitat expansion of the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea: potential consequences for the eelgrass food web. *BioInvasions Records* 5: 101–106, https://doi.org/10.3391/bir.2016.5.2.07

Haavisto F, Jormalainen V (2014) Seasonality elicits herbivores' escape from trophic control and favors induced resistance in a temperate macroalgae. *Ecology* 95: 3035–3045, https://doi.org/10.1890/13-2387.1

Hacker SD, Steneck RS (1990) Habitat architecture and the abundance and body-size-dependent habitat selection of a phytal amphipod. *Ecology* 71: 2269–2285, https://doi.org/10.2307/1938638

Hegele-Drywa J, Normant M (2009) Feeding ecology of the American crab *Rhithropanopeus harrisii* (Crustacea, Decapoda) in the coastal waters of the Baltic Sea. *Oceanologia* 51: 361–375, https://doi.org/10.5697/oc.51-3.361

Hegele-Drywa J, Normant M (2014) Non-native crab *Rhithropanopeus harrisii* (Gould, 1984) – a new component of the benthic communities in the Gulf of Gdánsk (southern Baltic Sea). *Oceanologia* 56: 125–139, https://doi.org/10.5697/oc.56-1.125

Honkanen T, Jormalainen V (2005) Genotypic variation in tolerance and resistance to fouling in the brown alga *Fucus vesiculosus*. *Oecologia* 144: 196–205, https://doi.org/10.1007/s00442-005-0053-0

Ikonen I, Hagelberg E (2007) Read up on reed! Southwest Finland Regional Environment Centre, Turku, Finland, 125 pp

Janas U, Kendzierska H (2014) Benthic non-indigenous species among indigenous species and their habitat preferences in Puck Bay (southern Baltic Sea). *Oceanologia* 56: 603–628, https://doi.org/10.5697/oc.56-3.603

Jordan F, Bartolini M, Nelson C, Patterson PE, Soulen HL (1997) Risk of predation affects habitat selection by the pinfish *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology* 208: 45–56, https://doi.org/10.1016/S0022-0981(96)02656-1

Jormalainen V, Gagnon K, Sjöroos J, Rothäusler E (2016) The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. *Biological Invasions* 18: 1409–1419, https://doi.org/10.1007/s10530-016-1090-9

Kallasvuo M, Lappalainen A, Urho L (2011) Coastal reed belts as fish reproduction habitats. *Boreal Environment Research* 16: 1–14

Karhilahti A (2010) Taskurapu tarttui pyydykseen. *Suomen Luonto* 4: 12–13

Kautsky H, Kautsky L, Kautsky N, Kautsky U, Lindblad C (1992) Studies on the *Fucus vesiculosus* community in the Baltic Sea. *Acta Phytogeographica Suecica* 78: 33–48

Korpinen S, Jormalainen V, Honkanen T (2007) Effects of nutrients, herbivory, and depth on the macroalgal community along a depth gradient. *Journal of Experimental Marine Biology and Ecology* 88: 839–852, https://doi.org/10.1890/05-0144

Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic – a sea of invaders. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1175–1188, https://doi.org/10.1139/f02-089

Levin P, Petrik R, Malone J (1997) Interactive effects of habitat selection, food supply and predation on recruitment of an estuarine fish. *Oecologia* 112: 55–63, https://doi.org/10.1007/s004420050283

Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619–640, https://doi.org/10.1139/z90-092

Long WC, Grow JN, Majoris JE, Hines AH (2011) Effects of anthropogenic shoreline hardening and invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*). *Journal of Experimental Marine Biology and Ecology* 409: 215–222, https://doi.org/10.1016/j.jembe.2011.08.024

Luppi T, Bas C, Méndez Casariego A, Albano M, Lancia J, Kittlein M, Rosenthal A, Farías N, Spivak E, Iribarne O (2013) The influence of habitat, season and tidal regime in the activity of the intertidal crab *Neohelice* (=*Chasmagnathus*) *granulate*. *Helgoland Marine Research* 67: 1–15, https://doi.org/10.1007/s10152-012-0300-9

Milke LM, Kennedy VS (2001) Mud crabs (Xanthidae) in Chesapeake Bay: claw characteristics and predation on epifaunal bivalves. *Invertebrate Biology* 120: 67–77, https://doi.org/10.1111/j.1744-7410.2001.tb00027.x

Molnar JL, Gamboa RL, Revenga C, Spalding MD (2008) Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment* 6: 485–492, https://doi.org/10.1890/070064

Nurkse K, Kotta J, Orav-Kotta H, Pärnoja M, Kuprijanov I (2015) Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisii* (Gould) in an invaded ecosystem: the north-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 154: 152–157, https://doi.org/10.1016/j.ecss.2014.12.046

Petersen C (2006) Range expansion in the northeast Pacific by an estuary mud crab – a molecular study. *Biological Invasions* 8: 565–576, https://doi.org/10.1007/s10530-005-0160-1

Richards RA (1992) Habitat selection and predator avoidance: ontogenetic shifts in habitat use by the Jonah crab *Cancer borealis* (Stimpson). *Journal of Experimental Marine Biology and Ecology* 156: 187–197, https://doi.org/10.1016/0022-0981(92)90245-6

Roche DG, Torchin ME (2007) Established population of the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841) (Crustacea: Brachyura: Xanthidae) in the Panama Canal. *Aquatic Invasions* 2: 155–161, https://doi.org/10.3391/ai.2007.2.3.1

Rodríguez G, Suárez H (2001) Anthropogenic dispersal of decapod Crustaceans in aquatic environments. *Interciencia* 26: 282–288

Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *American Zoologist* 37: 621–632, https://doi.org/10.1093/icb/37.6.621

Ryan EP (1956) Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. *American Midland Naturalist* 56: 138–162, https://doi.org/10.2307/2422450

Schubert K (1936) *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. *Zoologischer Anzeiger* 116: 320–323

Sih A (1980) Optimal behaviour: can foragers balance two conflicting demands? *Science* 210: 1041–1043, https://doi.org/10.1126/science.210.4473.1041

Sjöroos J (2016) Liejutaskuravun (*Rhithropanopeus harrisii*) tiheyden määrittäminen Saaristomeren liejupohjilla. Bachelor's Thesis, University of Turku, Turku, 14 pp

Stone RP, O'Clair CE (2001) Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. *Marine Ecology Progress Series* 214: 167–176, https://doi.org/10.3354/meps214167

Turoboyski K (1973) Biology and ecology of the crab *Rhithropanopeus harrisii* ssp. *tridentatus*. *Marine Biology* 23: 303–313, https://doi.org/10.1007/BF00389338

Verdolin JL (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology* 60: 457–464, https://doi.org/10.1007/s00265-006-0172-6

Vesakoski O, Merilaita S, Jormalainen V (2008) Reckless males, rational females: Dynamic trade-off between food and shelter in the marine isopod *Idotea balthica*. *Behavioural Processes* 79: 175–181, https://doi.org/10.1016/j.beproc.2008.07.005

Wahle RA, Steneck RS (1992) Habitat restrictions in early benthic life: experiments on habitat selection and in situ predation with the American lobster. *Journal of Experimental Marine Biology and Ecology* 157: 91–114, https://doi.org/10.1016/0022-0981(92)90077-N